Soil Water Stress and Photosynthesis in Cotton

By

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Abstract

An experiment was conducted in SPAR systems at Florence, S.C., to obtain a data set for use in the simulation of the effect of drying soil on photosynthetic rates in cotton. The plant water status was monitored using leaf water potential and stem diameter measurements. Reductions were noted in apparent photosynthesis rates after only 5 days of soil drying, and as anticipated, there was uniform displacement of the diurnal cycle of leaf water potential, and corresponding decreases in transpiration and CO_2 uptake. The photosynthesis-light response curves indicated that an average two-fold reduction in photosynthesis rates occurred for solar radiation greater than 250 W/m². Stem diameter change (from a nonstress pre-sunrise value) and integrated stem stress were found to be good indicators of maximum daily plant water stress. The integrated stem stress gave a measure of the duration of the stress along with its magnitude. A simulation method for predicting leaf water potential from stem diameter measurements was used to show that the magnitude and duration of plant water stress increased uniformly during the experiment. This increase was representative of the decreased rates of photosynthesis measured. These data will be used in the simulation of cotton growth and yield.

Introduction

The modeling of soil-plant-water relations requires that the effects of varying soil water potential upon basic physiological functions of the plant be understood and measured. Hsiao (1973) reported that alterations in metabolic processes resulting from water stress depended on the length and severity of the stress. One observable effect of changes in turgor due to water stress is reduced cell growth. Another is leaf photosynthesis.

Gaastra (1959) presented light response curves for leaves of various crop plants. At light saturation, the rate of photosynthesis was affected by the rate of CO_2 diffusion and, therefore, the CO_2 concentration. Under low light intensities, he found that the effect of stomatal resistance on photosynthetic rates was minimal and as the light intensities increased the effect of stomatal resistance on CO_2 diffusion rates increased. Photosynthetic rates of cotton have been shown to increase with CO_2 enrichment (Baker 1965). Over the range of 150 to 600 nl/l CO_2 in the canopy, Baker (1965) reported a linear trend in apparent photosynthesis for levels of solar radiation varying from 280 W/m² to 910 W/m².

Relationships between cotton yield and apparent photosynthesis were investigated by Baker et al. (1972). This research discussed the partitioning of photosynthates in relation to boll growth and respiration. The data were used in a dynamic simulation model of photosynthetic efficiency and yield of cotton (Baker et al. 1973). However, they could not be extended to include the effect of water stress on cotton photosynthesis.

Jordan and Ritchie (1971) measured diurnal variations in leaf water potential, diffusive resistance, relative water content, stem diameter, and energy balance components for field-grown cotton during water stress. They reported stomatal closure at leaf water potentials near −1600 kPa in their growth chamber study, though under field conditions minimum leaf water potentials reached −2700 kPa without stomatal closure.

Ackerson et al. (1977) reported that NO_3 reductase activity may be the inhibiting factor for photosynthesis when leaf water potentials are decreasing in field-grown cotton. Their data indicated that the stomata are relatively insensitive to leaf water potentials in the range of −1200 to −2800 kPa, and reductions in photosynthesis were not wholly attributable to stomatal closure resulting from plant water stress.

Research by Klepper et al. (1971) showed that the relationship between stem diameter and plant water status is susceptible to diurnal hysteresis, similar to that found in soil water. They reported that stem diameter and leaf water potential were closely related to net radiation, and they concluded that stem diameter measurements could be used to monitor long-term stem growth and plant water status.

Huck and Klepper (1977) presented two methods using stem diameter to predict the diurnal variation of xylem water potential. The first and simplest procedure, called the Shrinkage Modulus Method (Huck and Klepper 1977) deter-

mines an arbitrarily-calibrated shrinkage modulus and relates a measured change in stem diameter to a corresponding difference in leaf water potential. The modulus value is obtained by measuring the stem diameter and leaf water potential in early morning and in mid-afternoon and using their respective differences. However, the assumption that changes in stem diameter instantaneously follow changes in plant water potential makes accurate calibration difficult.

The second method, called the Dynamic Flux Method (Huck and Klepper 1978), simulates water flow between xylem and associated phloem parenchymal tissues, resulting from changes in plant water potential. Water potential differences between the xylem and surrounding tissues are assumed to induce a radial flux of water across the cambial boundary layer, causing swelling or shrinking of the stem. A value of xylem water potential that would induce a flux rate corresponding to the observed change in stem diameter is estimated by an iterative procedure for each successive time interval and the phloem potential is adjusted to approach the new xylem potential asymptotically.

Another method has been developed to simulate leaf water potential from stem diameter data (Personal communication with H. B. So, Department of Agronomy, University of New England, Armidale, New South Wales, 2531 Australia). This method attempts to correct the hysteresis-induced time lag between the stem diameter change and the corresponding change in leaf water potential using an analogy between the xylem-phloem-stem diameter and the tensiometer-soil system. This analogy has been used for cotton with reasonable success.

The objective of the research reported here was to develop a data set which, in a simulation model, will permit the calculation of the effects of continuously increasing soil water stress on the plant water status and the photosynthetic rate of cotton (*Gossypium hirsutum* L.) in the boll opening stage. In particular, the research deals with the relationships of stem diameter, leaf water potential, and soil matric potential profile with transpiration and photosynthetic rates.

Experimental Procedure

The experiment was conducted in controlled environmental chambers, the Soil-Plant-Atmosphere Research (SPAR) units, at Florence, South Carolina. Phene *et al.* (1978) described the SPAR units along with the measurement and control methods used.

Cotton (*Gossypium hirsutum* L. cv. Stoneville 213) was planted on day 164 1976 (12 June) and the experiment was conducted from day 285 to day 293 (11–19 October). The cotton was in the fruiting stage, and some of the bolls were opening.

The experimental procedure allowed the soil in SPAR unit B to dry naturally and continuously for the duration of the experiment.

Soil matric potentials (Ψ_s) were measured using heat dissipative soil matric potential sensors (Phene *et al.* 1971a,b; Model 2002 B, Watertech, Trinity, NC 27602). Nine sensors were installed in the soil at distances of 0, 0.25, and 0.50 m from the cotton row and at depths of 0.15, 0.45, and 0.80 m below the soil surface. Measurements were recorded hourly on a digital data acquisition system and were used to calculate the daily mean soil matric potential at each depth for SPAR unit B.

Solar radiation (R_i) was measured by an Eppley pyranometer mounted 2 m above the plants outside the SPAR units. Integrated measurements were recorded hourly by the data system.

The apparent net photosynthesis (P_N) was calculated every 30 min and summed for daily total, by measuring the time during which a known flow rate of the carbon dioxide (CO_2) was added to each of the SPAR units to maintain 300 nl/l (Phene *et al.* 1978). The flow rate was measured with a rotameter periodically throughout each day of the experiment. The apparent photosynthesis is calculated by the equation:

$$P_N = (V \times K \times C)/(t \times A) \qquad (1)$$

where P_N = apparent photosynthesis in mg $\text{min}^{-1}\,\text{m}^{-2}$ ground area, V = volume of CO_2 in cm^3, $K = 1.963$ (mg CO_2)(cm^3 CO_2)$^{-1}$, C = correction for the temperature and pressure of the flow, t = period of measurement in minutes, and A = soil surface area of the SPAR units, 1 m^2.

Transpiration from plants in each SPAR unit was measured by collecting the water condensed on the air conditioner coil in a vertical column and recording the level on the data system every 10 min (Phene *et al.* 1978).

The hydraulic pressure necessary to cause water flow from the uncut edge of the leaf was measured at sunrise and periodically each day to insure that maximum and minimum values were obtained. Measurements were made with a Model J-14 hydraulic press (Campbell Scientific Company, Logan, UT) at sunrise, after sunset, and during peak periods of stem diameter change. These pressure measurements were calibrated to leaf water potential, Ψ_L, by using a linear regression curve for conversion of hydraulic press to pressure bomb readings (Personal communication with D. C. Reicosky, Soil Scientist, USDA-AR, Morris, Minnesota 56267). Hydraulic press measurements have also been correlated with relative water content in leaves (Rhoades and Matsuda 1976). The hydraulic press was used since it is less destructive than other methods of measuring plant water potential.

The stem diameter changes (Δs) were measured with a DC-DC Transtek linear variable differential transformer with a holder designed to measure changes in the stem on which it is mounted (Klepper *et al.* 1971). These measurements were recorded manually from sunrise to sunset every 30 min with a digital voltmeter and continuously on a strip

chart recorder. The reference stem diameter, for computation of stem diameter change, was measured before sunrise on day 285 (*i.e.*, the stem diameter on non-water-stressed cotton) and was used throughout the experiment.

Stem diameter stress was integrated numerically using the equation:

$$ISS = \int_{t_0}^{t_1} \varDelta s_{(t)} \, dt \qquad (2)$$

where ISS = Integrated Stem Stress, in mm × day, t_0 = pre-sunrise time, in hours, t_1 = post-sunrise time, t, in hours, $\varDelta s_{(t)}$ = the stem diameter change, from the non-stress stem diameter, at time t, in mm.

This is very similar to the integrated stem stress presented by Browning *et al.* (1965). The difference is that the cotton stems in this study were shrinking and the base value was taken on day 285 at 7:00 EST as the non-stress stem diameter. After 3 days of soil drying, the stems began to shrink; therefore, this method reflects the duration and magnitude of plant water stress.

Results and Discussion

Table 1 presents the summarized daily measurements in SPAR unit B. Since the design of the SPAR units prevents soil evaporation and deep drainage from the soil compartment, measured soil drying is assumed to reflect plant water uptake and/or soil water movement. The soil dried rapidly near the surface. Soil at the 0.80 m depth did not substantially dry, thus indicating that the roots most active in water uptake were in the top two-thirds of the soil compartment and that the upward flux of water was too slow to keep up with the plant water uptake. On day 291, low solar radiation reduced transpiration to 0.2 mm/day. This reduction was not reflected in the rate of decrease in soil matric potential at 0.15 and 0.45 m soil depths, indicating that plants may have been attempting to recover from the plant water stress and that upward soil water movement was occurring too slowly.

A minimum observed $\varPsi_L$ of -2710 kPa was measured on day 292 (Table 1). This corresponded to a maximum $\varDelta s$ of 0.53 mm measured from the pre-sunrise stem diameter on day 285.

The relationship between the observed stem diameter change and the minimum observed $\varPsi_L$ is presented in Figure 1. The r^2 value for maximum stem diameter change versus minimum observed $\varPsi_L$ was 0.95. The regression of continuously observed $\varPsi_L$ versus observed $\varDelta s$ was not as good with an r^2 of 0.74 (Figure 2). The data point scatter was probably caused by two factors: (1) Experimental error in obtaining the leaf water potential values, and (2) The hysteresis induced by the plant xylem's resistance and capacitance to changes in the leaf water potential. The hysteresis between stem diameter and leaf water potential were observed by Klepper *et al.* (1971) and Huck and Klepper (1977).

Huck and Klepper (1977) have suggested simulation methods for calculating $\varPsi_L$ from stem diameter measurements. The dynamic flux method (Huck and Klepper 1977) does not correct for the hysteresis in the system; thus we chose the method discussed in the introduction, since this method attempts to correct for hysteresis.

A simulation of $\varPsi_L$ was done for days 288 and 292. We chose these 2 days because both days were clear and the
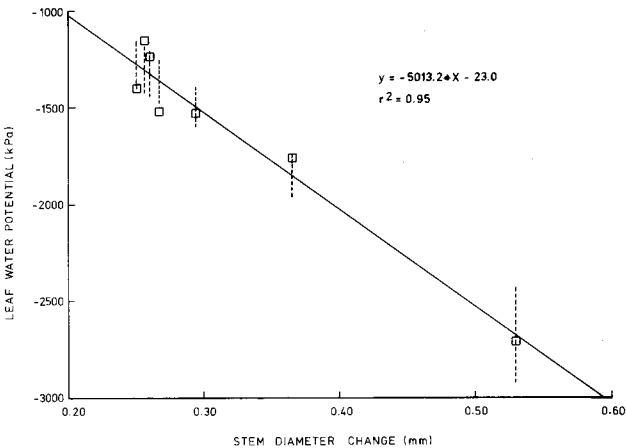

Figure 1. *Linear regression of minimum observed leaf water potential vs. maximum stem diameter change from the reference stem diameter.* Broken lines represent 90% confidence intervals based on the regression analysis.

In the figure: $y = -5013.2 * X - 23.0$, $r^2 = 0.95$

Table 1. *Daily measurements in SPAR Unit B.* ** indicates measurement not taken.

| Day	Average R_i W/m²	P_N g CO_2/m² of soil area × day	Transpiration mm	$\varPsi_S$ (kPa) 0.15 m	0.45 m	0.80 m	Minimum $\varPsi_L$ kPa	Maximum $\varDelta s$ mm	mm · day
285	436	47.5	**	−30	−48	−9	−1150	0.26	2.02
286	442	38.3	9.8	−57	−47	−9	−1400	0.25	2.06
287	427	36.8	7.0	−164	−50	−12	−1520	0.27	2.11
288	425	33.6	6.0	−207	−54	−12	−1530	0.29	2.18
289	392	34.5	5.2	−255	−74	−12	−1760	0.37	2.92
290	358	27.4	3.0	−288	−103	−13	**	0.30	2.59
291	51	20.8	0.2	−416	−152	−15	**	0.19	1.79
292	440	18.9	2.7	−686	−275	−18	−2710	0.53	4.94
293	257	16.4	3.0	−722	−261	−19	**	0.34	3.62
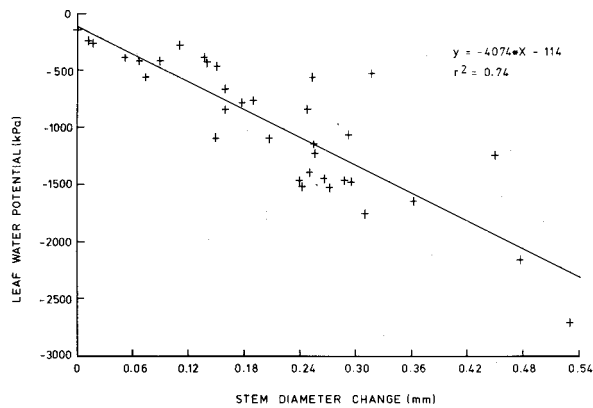
Figure 2. *Linear regression of leaf water potential vs. stem diameter change.*

solar radiation was relatively high. On day 288, the soil was dry near the surface (−207 kPa), but had not changed substantially at the 0.45 and 0.80 m depths (−54 and −12 kPa, respectively) from what it was at the start of the experiment (−48 and −9 kPa, respectively). The maximum Δs, ISS, and minimum calculated Ψ_L showed little indication of plant water stress on day 288. On day 292, the plant parameters indicated severe plant water stress. The minimum Ψ_L was −2710 kPa and the stem diameter and integrated stem stress value were double those at the beginning of the experiment.

The simulated leaf water potentials using this method for day 288 and 292 are presented in Figure 3. This method depends largely on the estimation of phloem potential, by using the rate of the phloem potential changes with respect to the stem diameter, $d\Psi/ds$. For day 288, a hysteresis time lag of 0.3 h, and for day 292 a hysteresis time lag of 0 h were estimated by using the solar radiation and stem diameter. The $d\Psi/ds$ value on day 288 was 5370 kPa/mm as compared with 5108 kPa/mm on day 292. These data indicated that the entire diurnal cycle of leaf Ψ_L shifts lower as the magnitude of the water stress increases. Thus, as the minimum Ψ_L decreases, the early morning values also
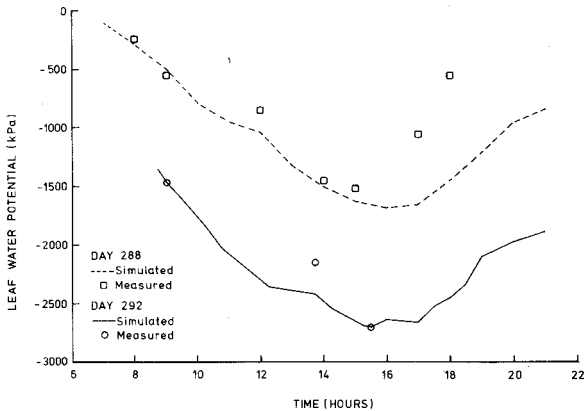
decrease as was shown in soybeans by Heatherly *et al.* (1977). Morning Ψ_L values were −280 kPa on day 288 and −1400 kPa on day 292. The simulated values on day 288 agreed well with observed values of Ψ_L for the morning. Apparently, this method of accounting for a dynamically changing time lag between the xylem tissue and the phloem tissue due to nonconstant conductivity (as suggested by Parlange *et al.* 1975) is not entirely successful, since some divergence from the simulation occurred in the afternoon on day 288. Nevertheless, we believe this method may serve well enough to estimate leaf water potential in a crop simulation model. The simulated values of Ψ_L for day 292 agreed well with those measured. A comparison of simulated Ψ_L on these 2 days indicated that the effect of severe plant water stress resulted in an overall Ψ_L decrease uniformly throughout the day.

The decreases observed in the simulated Ψ_L values are also evident in the light response curves for day 288 and 292 (Figure 4). A comparison of the 2 days indicates that a decrease in P_N rate occurred for levels of solar radiation greater than 250 W/m². This reduction was uniform for higher values of solar radiation. It is worth emphasizing that this reduction in P_N rates (on day 292 as compared with day 288) occurred after only 5 days of soil drying and even
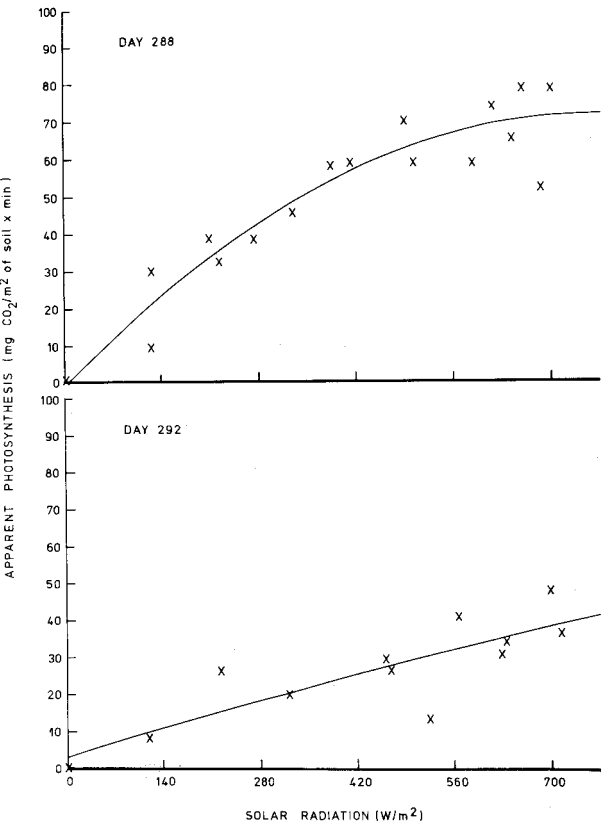

Figure 3. *Simulated leaf water potential vs. time.*

Figure 4. *Apparent photosynthesis in cotton as a function of solar radiation for days 288 and 292.*
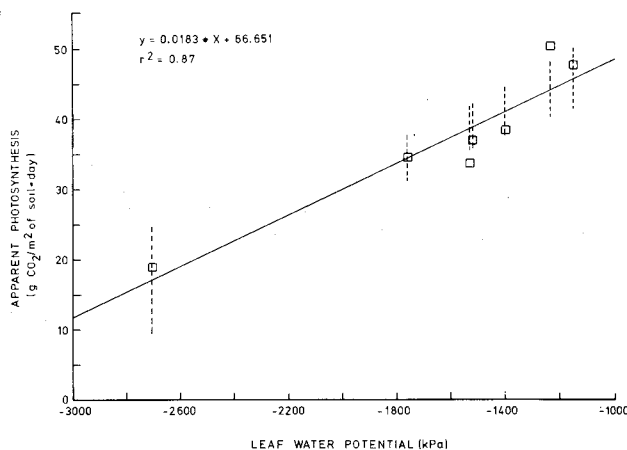
Figure 5. *Linear regression of daily apparent photosynthesis vs. minimum observed leaf water potential.* Broken lines represent 90% confidence intervals based on the regression analysis.

though the soil matric potential at 0.80 m was relatively high (−19 kPa).

Figure 5 presents the relationship for the total daily photosynthate production vs. minimum Ψ_L (data plotted only for days with 391 W/m^2 or greater average solar radiation levels). For minimum leaf water potential ranging from −1200 to −2710 kPa, the regressed slope coefficient for CO_2 reduction vs. Ψ_L was 0.0183 g CO_2/m^2 ground area day per kPa decrease of Ψ_L. The r^2 value for P_N vs. Ψ_L was 0.87 (Figure 1)

The maximum Δs, ISS, and minimum Ψ_L indicated that the plants were under progressively greater plant water stress (Table 1). The magnitude and duration of the plant water stress is shown in the decrease of total P_N values on days 290 and 292 (Table 1). After day 291, an overcast day, the P_N rate continued to decrease on day 292 from the P_N rate on day 290. Transpiration was reduced to about 3.0 mm on day 290, 292, and 293 (Table 1), indicating that the stomates were at least partially limiting even though the bottom of the root zone was nearly saturated.

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Edited by A.K.